Population Growth Characteristics of Incipient Colonies of the Eastern Subterranean Termite, *Reticulitermes flavipes* (Isoptera: Rhinotermitidae)

A Senior Honors Thesis

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ABSTRACT

Growth of *Reticulitermes flavipes* incipient colonies was documented for their first year. Each month, 15 established colonies, each headed by a queen and king pair, were censused, with data obtained for the number of individuals of each caste and/or developmental stage and their collective mass. The mass of the king and queen was individually measured. A grand total of 180 colonies was examined.

Egg production was intermittent during the first year, with the greatest number of eggs (mean = 14.5) produced during the first month. Three cohorts of eggs were produced and egg production was not constant

Larvae were observed at 1 mo and workers (> second instar) were first observed at 2 mo. The survival rate of the initial brood was less than 100%, since the average number of eggs, larvae, and workers in the first two months decreased during the following months. At the 6-mo census, a soldier was observed in each of two colonies with total populations of 12 and 13 individuals. Soldiers were sporadically present in colonies thereafter and the number of colonies containing a single soldier increased at the 12-mo observation. One-year-old colonies ranged in size from 20 to 40 individuals, including the king and queen, with an average of 28.9 individuals.

King and queen mass greatly decreased during the first two months, coinciding with egg production and colony foundation, and their mass remained relatively constant through the 12-mo observation. Offspring biomass was equal to that of the reproductive pair at the 2-mo census, double at 3 mo, and quadruple at 11 mo. Total biomass of each colony gradually increased over time. The average biomass of a 1-yr-old colony was 39.8 mg.

The growth rate observed in this study was much slower than that observed by others (Snyder and Popenoe 1932, Grube and Forschler 2002). Overall, this study's results are

consistent with previous models and suggestions regarding colony growth (Grube and Forschler 2004, Suiter et al. 2002), but this study provides the numerical data.

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CHAPTER 1: INTRODUCTION AND LITERATURE REVIEW

1.1 Termite biology

Termites are a social insect that have a very complex life cycle. As defined by sociality, termites (Isoptera) share resources, cooperate in responsibilities of rearing young, and have overlapping generations and a division of labor (Suiter et al. 2002).

Termites are grouped phylogenetically into the lower termites (Mastotermitidae, Termopsidae, Hodotermitidae, Kalotermitidae, Serritermitidae, and Rhinotermitidae) and the higher termites (Termitidae) (Kambhampati and Eggleton 2000). The lower termites utilize protozoan gut symbionts in order to digest cellulose whereas the higher termites lack symbiotic protozoans and rely solely on prokaryotic gut symbionts and endogenous cellulases (Bignell 2000). The higher termites account for approximately 75% of all termite species and have diverse feeding habits with some species feeding on fungi, soil, or cellulose materials (Krishna 1969).

As social insects, termites have a caste system. The caste of each individual is determined during post-embryonic development (Laine and Wright 2003) depending on the various pheromones present in the colony (Suiter et al. 2002). In some rhinotermitid species, there also is a sexual bias to caste determination with an equal number of male and females becoming workers, but soldiers being female biased and nymphs being male biased (Hu and Forschler 2012).

The division of labor in termite colonies consists of the worker, soldier, and reproductive caste, each with their own tasks. Each caste can be visually differentiated by several key traits. Workers of the lower termites typically are unpigmented and white, and they lack eyes and they show no signs of wing development. Soldiers have an enlarged and sclerotized head capsule and mandibles to aid in colony defense. The reproductive caste has multiple forms (reviewed by Thorne 1996) but the exoskeleton is sclerotized to some extent.

The primary reproductives (king and queen) are alate derived and hence show evidence of wings (i.e., wing scales); they have fully developed eyes and are fully pigmented. Neotenic reproductive are often found in termite colonies, particularly those where the king and/or queen had died or is missing, and are non-alate derived and never have fully developed wings or eyes; they can be slightly or heavily pigmented. Nymphoid reproductives develop from the nymphal stage and have wing pads, but they do not have many of the mature characteristics of a primary reproductive. Ergatoid reproductives are worker-derived neotenics that are smaller than nymphoid reproductives and lack wing buds (Thorne 1996).

1.2 Colony establishment

In order to colonize new resources, swarm events occur where winged reproductive termites disperse to initiate new colonies (Snyder 1915). In these swarms, both male and female winged adults typically disperse simultaneously from the colony. Male and female termites then pair off, shed their wings, and create a nest (Suiter et al. 2002). The pair mates in this incipient nest, rather than in their natal nest (Dean and Gold 2004, Ye et al. 2009). The newly mated queen lays eggs, and accompanied by the king, growth of the new colony begins (Snyder 1915).

1.3 Studies of early termite colony development in the Rhinotermitidae

Development of colonies headed by a single primary pair (queen and king) has been investigated to some extent for numerous species of subterranean termites. The Formosan subterranean termite, *Coptotermes formosanus,* is a well-studied species (King and Spink 1974, 1975; Suiter et al. 2002; Fei and Henderson 2003; Morales-Ramos and Rojas 2003; Sun 2007) that was introduced into the southern United States after World War II. Initial colony growth also has been studied for the western subterranean termite, *Reticulitermes hesperus*, with a focus on the production of soldiers (Light and Weesner 1955). Early colony development in the eastern subterranean termite, *Reticulitermes flavipes*, has been investigated (Snyder and Popenoe 1932, Thorne et al. 1997, Grube and Forschler 2002) but further research is necessary. Overall, these studies provide background information into the dynamics of a subterranean termite colony during the first year of development.

1.3.1 *Coptotermes formosanus:* King and Spink (1974, 1975) thoroughly investigated the initial colony growth characteristics of *C. formosanus* in a laboratory and field setting in southern Louisiana. King and Spink (1974) observed four distinct oviposition periods in the 2.5-year duration of their study. Nest excavation did not continue after the initial establishment until young reached the worker stage and were able to assist in colony tasks (King and Spink 1975). The soldier caste consisted of approximately 10 percent of the colony, but initial soldiers formed in the colony were significantly smaller than the soldiers produced in a mature colony (King and Spink 1974).

Environmental factors affecting *C. formosanus* colony development were investigated by King and Spink (1974, 1975). Temperature was positively correlated with the development rate, but significantly more mortality occurred at 32°C than 26°C. Also, oviposition did not occur at temperatures lower than 21.5°C or in field colonies during winter conditions (King and Spink 1974, 1975).

Inbred colonies of *C. formosanus* proved to have a higher survival rate than outbred colonies. However, the overall fitness of inbred colonies was lower given that they produced a significantly smaller number of workers and larvae (first and second instar termites) than outbred colonies for the first six months of development (Fei and Henderson 2003).

Studies of *C. formosanus* have investigated food preference and the effect of food type on colony development (Morales-Ramos and Rojas 2003, Sun 2007). Morales-Ramos and Rojas (2003) compared the survival and growth of incipient colonies reared on 11 different types of wood. They found that colonies feeding on pecan (*Carya illinoensis*) and red gum (*Liquidambar styraciflua*) produced the most progeny. Those feeding on pecan and American ash (*Fraxinus americana*), however, had the highest survival rate. Using various choice tests, they concluded that the nutritional value of the food source determined the termites' feeding preference. In a similar study, Sun (2007) investigated the nutritional ecology of various landscape mulches. He found that the survival rate was the highest on pine (*Pinus* sp.) straw, eucalyptus (*Eucalyptus* sp.), bald cypress (*Taxodium distichum*), and water oak (*Quercus nigra*) compared to pine bark, cedar (*Juniperus* sp.), and melaleuca (*Melaleuca quinquenervia*). Hence, selection of a particular landscape mulch can affect the rate of termite infestation.

1.3.2 *Reticulitermes hesperus:* Light and Weesner (1955) investigated the development of *R. hesperus* colonies but primarily focused on the production of soldiers. They found that not all colonies produce a soldier in the first cohort of eggs, disproving previous assertions. The early presence of soldiers was common to groups of colonies but they could not determine the cause of the soldiers' presence.

1.3.3 *Reticulitermes flavipes:* Snyder and Popenoe (1932) reported casual observations on laboratory colonies of *R. flavipes*. Clusters of eggs (unspecified number of eggs) were not observed until 12 days after mating. Six days later, two clusters of eggs were present in most colonies. After one month, larvae were present, and in the second month, a new cohort of eggs was present as well as many larvae. During the third month, they observed workers as well as larvae, and the first soldiers were present during the sixth month. At various times, cannibalism was observed, with termites feeding on healthy larval termites even in the presence of an abundant food source.

On average, it is thought to take approximately 5-10 years for the colony to mature and form alates (Su et al. 2009). A few laboratory-reared intact *R. flavipes* colonies produced alates 8 years after establishment of the primary pair (Jones, unpubl. obs.).

Thorne et al. (1997) further investigated *R. flavipes* development and arrived at similar conclusions to those of Snyder and Popenoe (1932). A total of 200 two-year-old incipient *R. flavipes* colonies were destructive sampled and observed to range in size from 51 to 984 individuals, with a mean of 387 colony members. The average number of workers was 322. The average number of soldiers was 6.8, or about 2.1 percent of the colony. Although Thorne et al. (1997) did not monitor colonies of different ages, their study provided insight into colony size after two years.

Another study focusing on *R. flavipes* investigated population growth comparing monogamous and polygynous pairs of reproductives (Grube and Forschler 2004). To compare these reproduction strategies, colonies were established with varying reproductive ratios and censused every four months. Polygyny was maintained in only 9.7% of the colonies after four months, and in most colonies, the initial multiple reproductives were reduced to a single pair. In the monogamous colonies, soldiers were present in most of the colonies four months after establishment. After one year, the number of workers ranged from 15 to 259. However, Grube and Forschler (2004) did not provide average colony size of those initially headed by multiple reproductives versus a single pair.

1.4 Test organism

R. flavipes is an economically significant pest species that is widely distributed in the eastern United States. Approximately $11 billion is spent annually to prevent and treat subterranean termites and to repair their damage (Su 2002), thus, termites are a significant economic pest in the United States. The current research allows for a better understanding of the biology of these termites, which may provide further insights into basic research. *R. flavipes* is a suitable test organism because it is a good representative of subterranean termites and a very widespread pest in the United States.

CHAPTER 2: POPULATION GROWTH CHARACTERISTICS OF INCIPIENT TERMITE COLONIES

2.1 Introduction

The subterranean termites (Rhinotermitidae) are significant pest species that are widespread in the United States costing more than $11 billion dollars annually (Su 2002). The life cycle of subterranean termites is complex but critical to understanding the establishment and spread of this pest.

The termite life cycle begins with the dispersal of winged alates to colonize new resources. The alates pair, shed their wings, and establish a new nest (Suiter et al. 2002). The castes are determined during post-embryonic development and each larva (first or second instar termite) can become a worker, soldier, or reproductive (Laine and Wright 2003).

The reproductive caste can have multiple forms (reviewed by Thorne 1996). The primary reproductives are alate derived and are the king and queen in the colony. A neotenic reproductive is a reproductive that is not derived from an alate and still retains some juvenile characteristics. Secondary, or nymphoid reproductives, are neotenics derived from nymphs. These have wing pads and their body pigmentation is generally a yellow hue. Tertiary, or ergatoid reproductives, are those derived from workers. These are generally smaller than nymphoid reproductives and are apterous with very light pigmentation (Dombrowski 2005).

Early colony development has been studied in various rhinotermitids. For example, alate-founded colonies have been studied for *C. formosanus* (King and Spink 1974, 1975; Fei and Henderson 2003; Morales-Ramos and Rojas 2003; Sun 2007), *R. hesperus* (Light and Weesner 1955) and *R. flavipes* (Snyder and Popenoe 1932, Thorne et al. 1997, Grube and Forschler 2002) but further research is necessary. Colony development from groups of workers and nymphs has been studied in *R. urbis* (Ghesini and Marini 2009).

R. flavipes incipient colony growth has been studied by various researchers. Snyder and Popenoe (1932) observed laboratory-reared colonies and documented the abundance of castes at various times. Thorne et al. (1997) used a destructive sampling technique to census two-year-old colonies, noting the abundance of castes and colony size range. Grube and Forschler (2004) studied incipient colony growth of monogamous and polygynous colonies during the first two years.

2.2 Objectives and Hypothesis

The objectives of this observational study were to investigate population growth dynamics of *R. flavipes* colonies during the first year through the parameters of numbers, castes and/or developmental stages, and biomass. Based on the relevant literature, I hypothesized that colony development would be very similar to the previous assertions but more insights would be gained by intensively focusing on the first year of development.

2.3 Materials and Methods

2.3.1 Experimental Setup: Thousands of *R. flavipes* alates were collected from a single swarm that occurred in Pickaway County, Ohio, on 20 May 2011. The swarm was from a presumably large colony and it originated in a barn on a rural farm. The termites were individually sexed by examining the VIII – X abdominal sternites. In the Isoptera, the female alates lack styli and have a noticeably elongated IX abdominal sternite compared to the males (Jones and La Fage 1980, Zimet and Stuart 1982, Roisin and Lenz 1999).

Each male and female pair was then placed into a “nest” container (3.8 cm ht x 5.4 cm dia, with lid) that had been lined with a moist filter paper pad and provisioned with a combination of moist soft and hardwood mulch. Hundreds of colonies were maintained in the lidded containers in an environmental chamber in the dark at 26º C with 85-90% relative humidity. Water was added to the colonies as needed throughout the study.

2.3.2 Census Methods: Fifteen different colonies were randomly selected to be censused monthly for a 1-yr period, but only visually established colonies headed by a single queen and king were examined. Data were recorded for all castes in each colony including the number of individuals and their collective mass; the mass of the king and queen was individually obtained. Each colony was reestablished after censusing, but no colony was resampled during the study. A grand total of 180 colonies was examined.

2.4 Results

Throughout the first year of colony development, the number of individuals varied dramatically from month to month (Figure 1). As seen in Table 1, the general colony trends are paralleled in related studies (Snyder and Popenoe 1932, Dombrowski 2005).

Egg production was intermittent, with the greatest number of eggs (mean = 14.5) produced during the first month (Figure 1). As shown in Figure 2, there were three cohorts of eggs; the first was large (mean = 19.2) and occurred during the first and second month, the second was very small (mean = 3.6) and occurred in the sixth and seventh month, and the third was moderate but broad (mean = 19.6), spanning months nine through twelve. Egg production was not constant during the first year of development

Larvae were observed at 1 mo and workers were first observed at 2 mo (Figure 2). The number of larvae in the colony remained between 0 and 3, with the exception of the initial cohort which consisted of 7.6 larvae at the 2-mo observation (Figure 2). The number of workers ranged from 8.1 at the 2-mo observation to 18 workers at the end of the 1 yr study. The survival rate of the initial brood was less than 100%, since the average number of eggs, larvae, and workers in the first two months decreased during the following months (Figure 1).

At the 6-mo census, a soldier was observed in each of two colonies with total populations of 12 and 13 individuals. Soldiers were sporadically present in colonies thereafter and increased in abundance at the 12-mo observation (Figure 3). Overall, soldiers averaged less than 1% of the 1-yr-old colony.

The mass of both the king and queen greatly decreased during the first two months, coinciding with egg production and colony foundation, and remained relatively constant thereafter through the 12-mo reading (Figure 4). The total mass of each colony gradually increased over time and consisted primarily of the worker caste in 1-yr-old colonies (Figure 5). Offspring biomass was equal to that of the reproductive pair at the 2-mo census, double at 3 mo, and quadruple at 11 mo (Figure 6).

2.5 Discussion

Overall, the results obtained in my intensive study of *R. flavipes* incipient colonies during their first year of development support previous models and assertions regarding colony growth, but my study provides the numerical data to support the claims. Several distinct trends are revealed by the data. Egg production was intermittent throughout the first year of *R. flavipes* colony development, with several distinct cohorts of eggs as well as periods without eggs (Figure 2). This implies that the king and queen partition their initial investment between reproduction and initial brood care. Eventually, as the colony grows, brood care tasks will be taken over by workers, then egg production is expected to become continuous (Suiter et al. 2002).

Based on the trends in reproductive biomass, one assertion for the dramatic decrease in mass of both the male and female *R. flavipes* reproductive is their potential use of fat stores to foster the developing young. Their most dramatic mass decrease occurred in the first 2 mo (Figure 4), which corresponds with the first and largest cohort of eggs (Figure 2) and the initial care of these young. The reproductives' mass continued to decrease until month 4 when the initial cohort of workers (mean = 12.7) was present in the colony (Figure 3). Workers' duties include assisting in nest construction and brood care.

Figure 1 reveals that there was an initial peak in total colony members that decreased dramatically from 22.3 to 13.9 between the second and fifth months. This sharp decline indicates that not every egg hatched and not every worker survived. Likewise, Snyder and Popenoe (1932) observed cannibalism of larvae in young colonies, and this may have been a contributing factor.

Trophic eggs are known in some social Hymenoptera where the queen lays eggs to convert her fat stores into a food source for the developing colony (Brian and Rigby 1978). However, there are no published reports of trophic eggs in *R. flavipes*, and Yamamoto and Matsuura (2011) indicated that they did not occur in a closely-related species, *R. speratus*. Hence, it is unlikely that trophic eggs contributed to the decline in numbers observed in my study.

The growth rate of *R. flavipes* incipient colonies observed in my study was much slower than that observed by others (Snyder and Popenoe 1932, Grube and Forschler 2002). Table 1 shows that after 1 yr, there were many fewer termites (mean = 28.9) than were observed by Dombrowski (2005) (mean = 89.2). Many factors could have caused this including simple colony variation. In addition, temperature and food source could have been contributing factors. For example, Grube and Forschler (2002) used a mixture of sawdust as a food source compared to my study which used a mixture of soft and hardwood mulch, which may be more difficult for digestion. Snyder and Popenoe (1932) reported that the initial clutch of eggs was "the size of small peas" which may have been much larger than what was observed in my study, depending on the pea species. The slower growth rate also may be attributable to the inbred *R. flavipes* reproductives, similar to Fei and Henderson's (2003) conclusion that inbred *C. formosanus* have lower fitness than outbred colonies.

Soldiers also were present during the first year in Grube and Forschler's (2004) study, but they observed larger numbers (3.0% at 1 yr) than in my study (<1% at l yr). The appearance of soldiers later in the first year is consistent with Light and Weesner's (1955) conclusions for *R. hesperus* that certain unknown conditions cause a group of colonies to produce soldiers either in the initial cohort or in the second cohort. However, Snyder and Popenoe (1932) found similar results with soldiers first observed in 7 mo colonies (table 1)

2.6 Conclusions and directions for future study

Overall, my study reveals similar growth trends as observed in previous studies of *R. flavipes* (Snyder and Popenoe 1932, Grube and Forschler 2002) and related species (*C. formosanus*: King and Spink 1974, 1975, Fei and Henderson 2003, Morales-Ramos and Rojas 2003, Sun 2007; *R. urbis:* Ghesini and Marini 2009; and *R. hesperus:* Light and Weesner 1955). Although the colony growth during the first year was slower in my study than many others, the general trends still prevailed.

Although this research focused on the first twelve months of *R. flavipes* colony development, many factors could be varied to better understand their impact on colony development. Studies of *C. formosanus* have analyzed food preference (Morales-Ramos and Rojas 2003, Sun 2007), but this has not been well studied for *R. flavipes*. Also, the effect of food availability as well as the "nest" container size would be topics for future research. The changes in development based on temperature and humidity have been documented in *C. formosanus*

(King and Spink 1974), and this also would be an interesting direction for future research with *R. flavipes.*

Table 1: Comparison of previous studies regarding *R. flavipes* colony growth during the first year

	Snyder and Popenoe (1932)	**Dombrowski (2005)**	**Janowiecki et al.**
Number of colony members after 12 months	Not reported	89.2 (average) N=57 colonies	28.9 (average) N=15 colonies
Appearance of soldier caste	7 months	Not reported	6 months

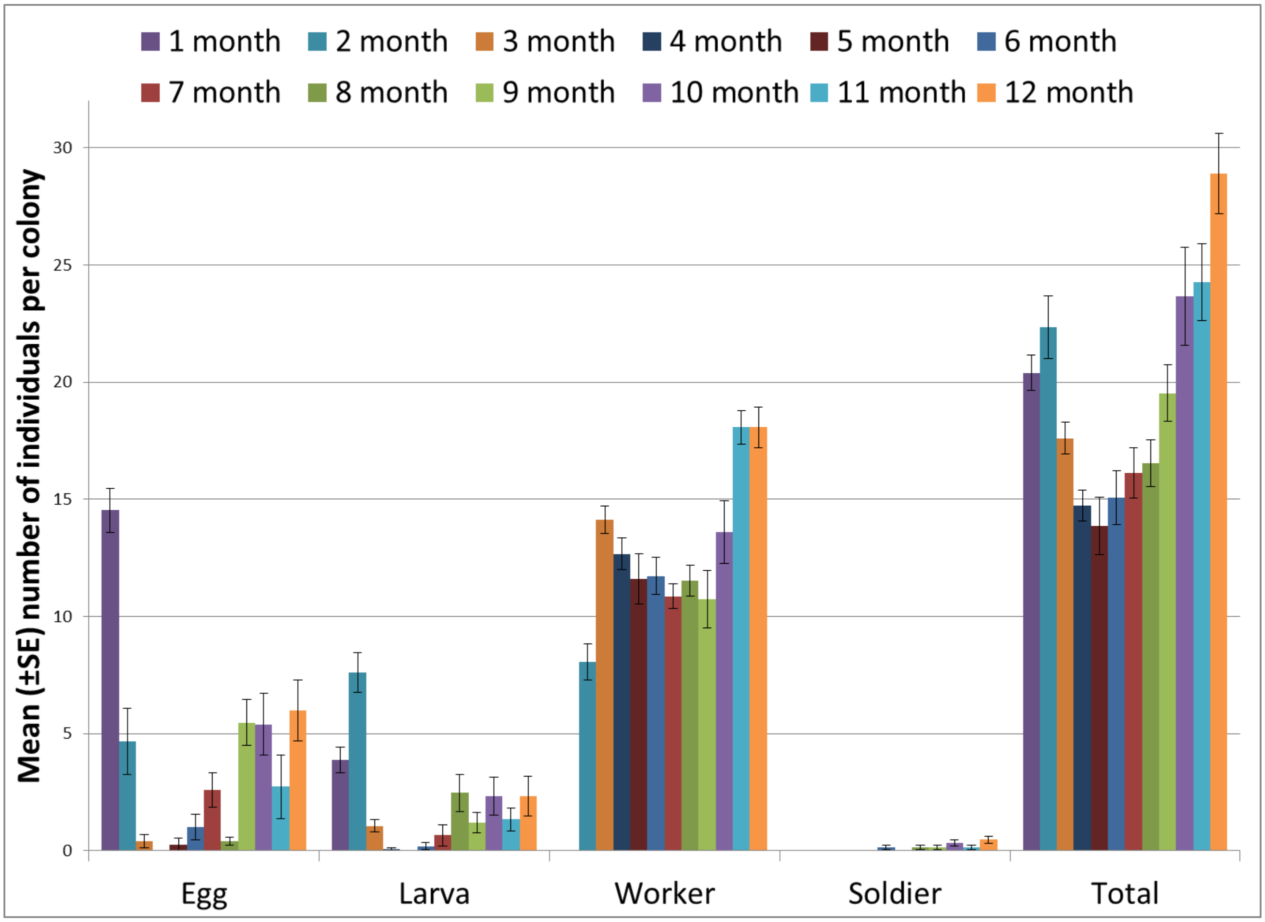

Figure 1: Numbers of Each Caste and/or Developmental Stage at Monthly Intervals During the First Year of Incipient Colony Growth.

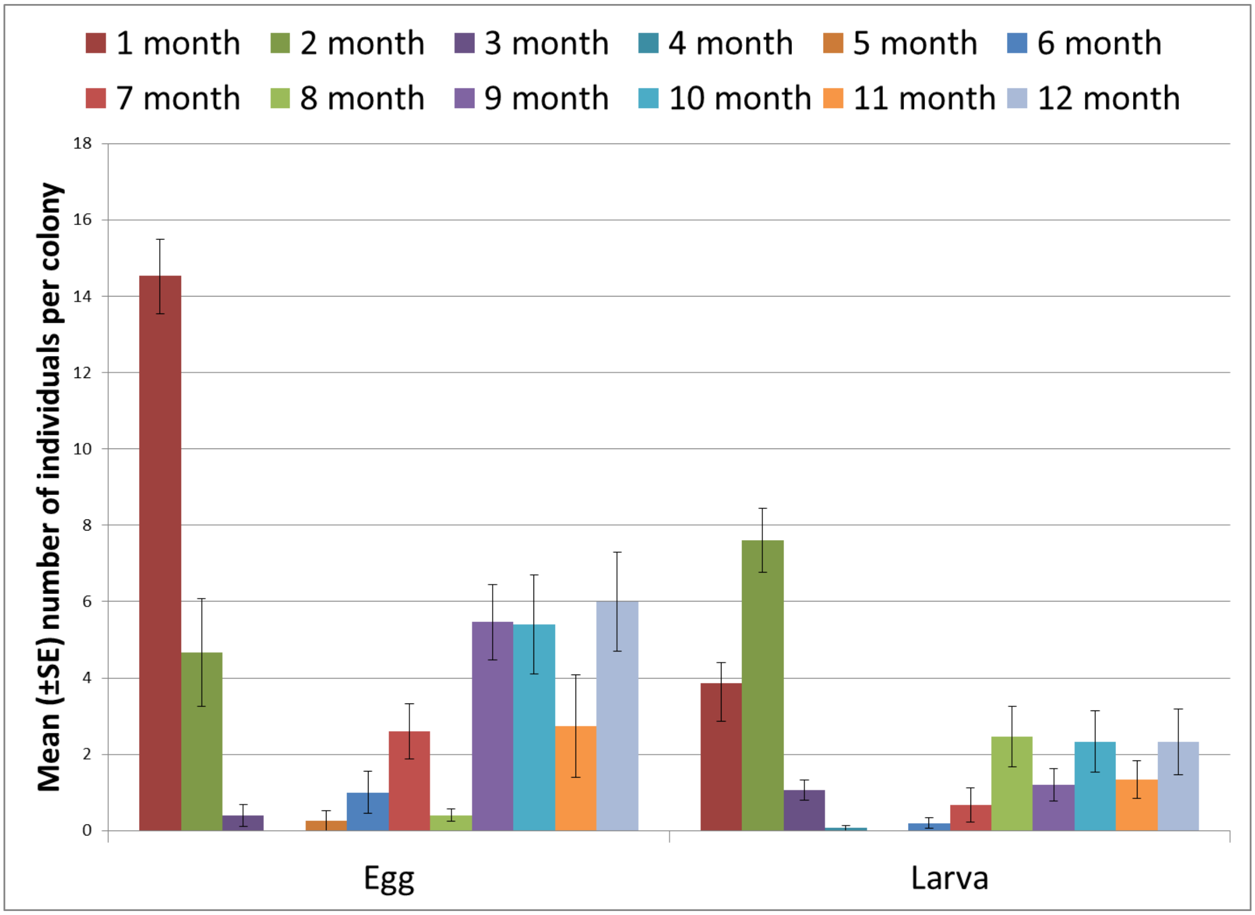

Figure 2. Numbers of Eggs and Larvae at Monthly Intervals During the First Year of Incipient Colony Growth.

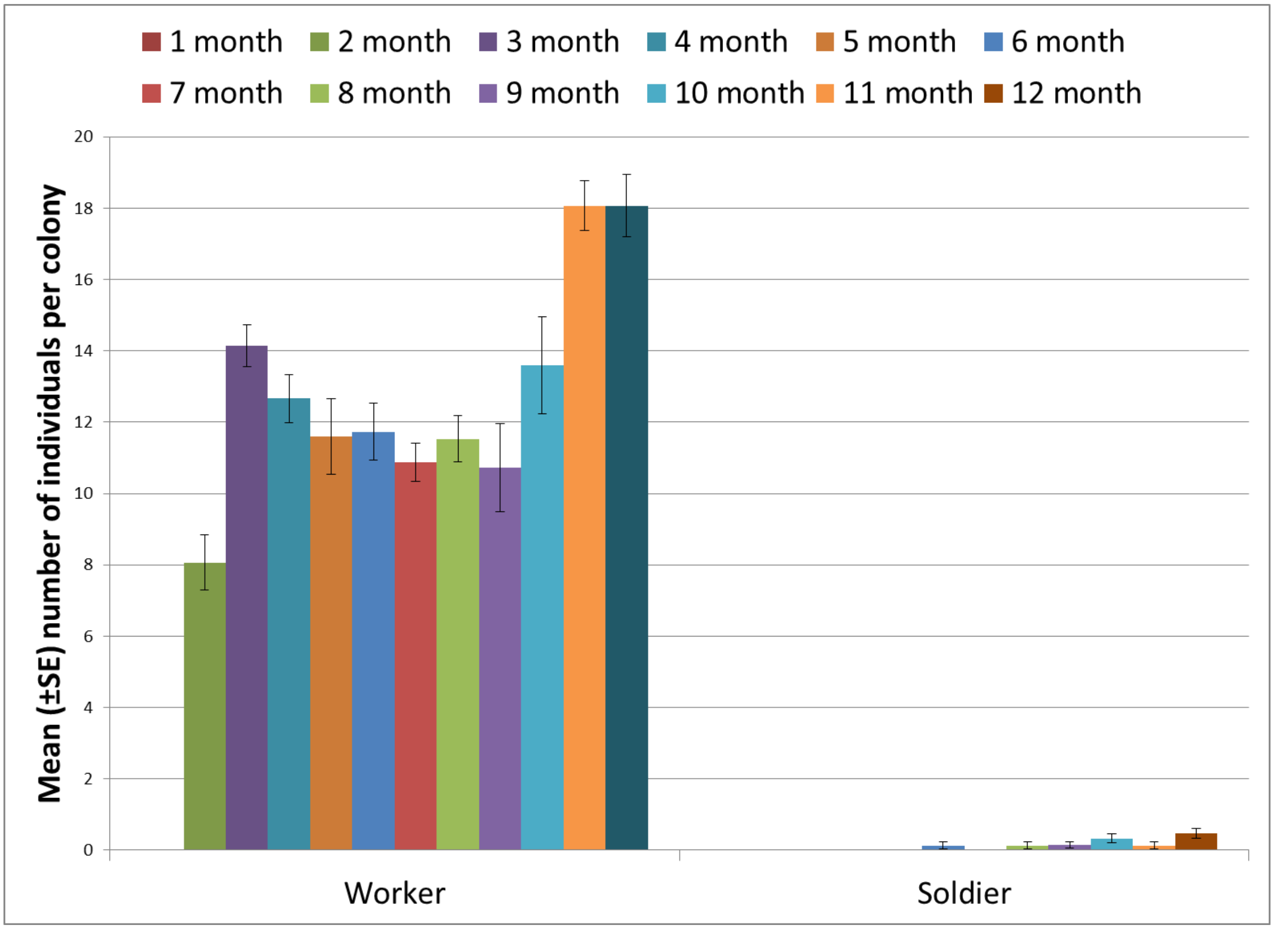

Figure 3. Numbers of Workers and Soldiers at Monthly Intervals During the First Year of Incipient Colony Growth.

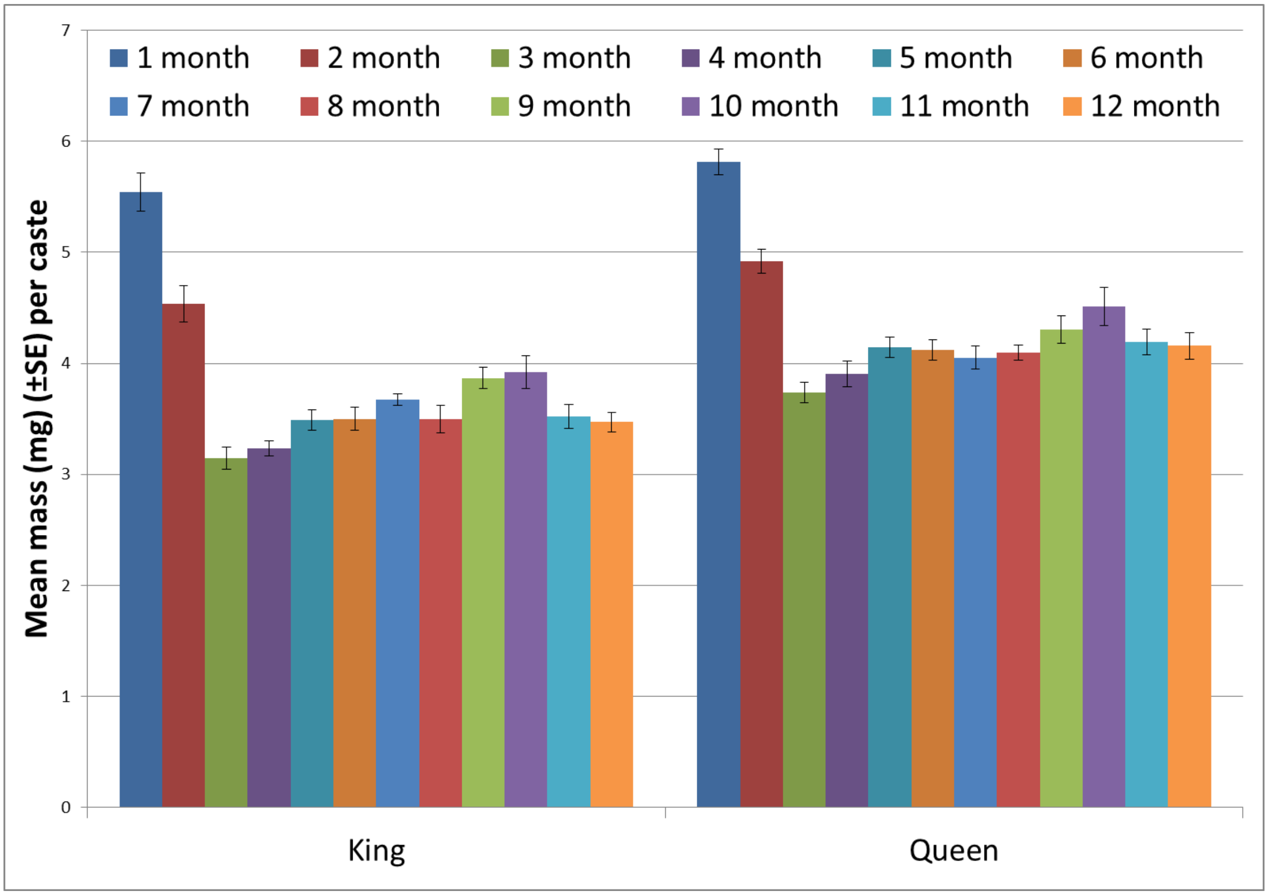

Figure 4. Biomass of the Primary Pair at Monthly Intervals During the First Year of Incipient Colony Growth.

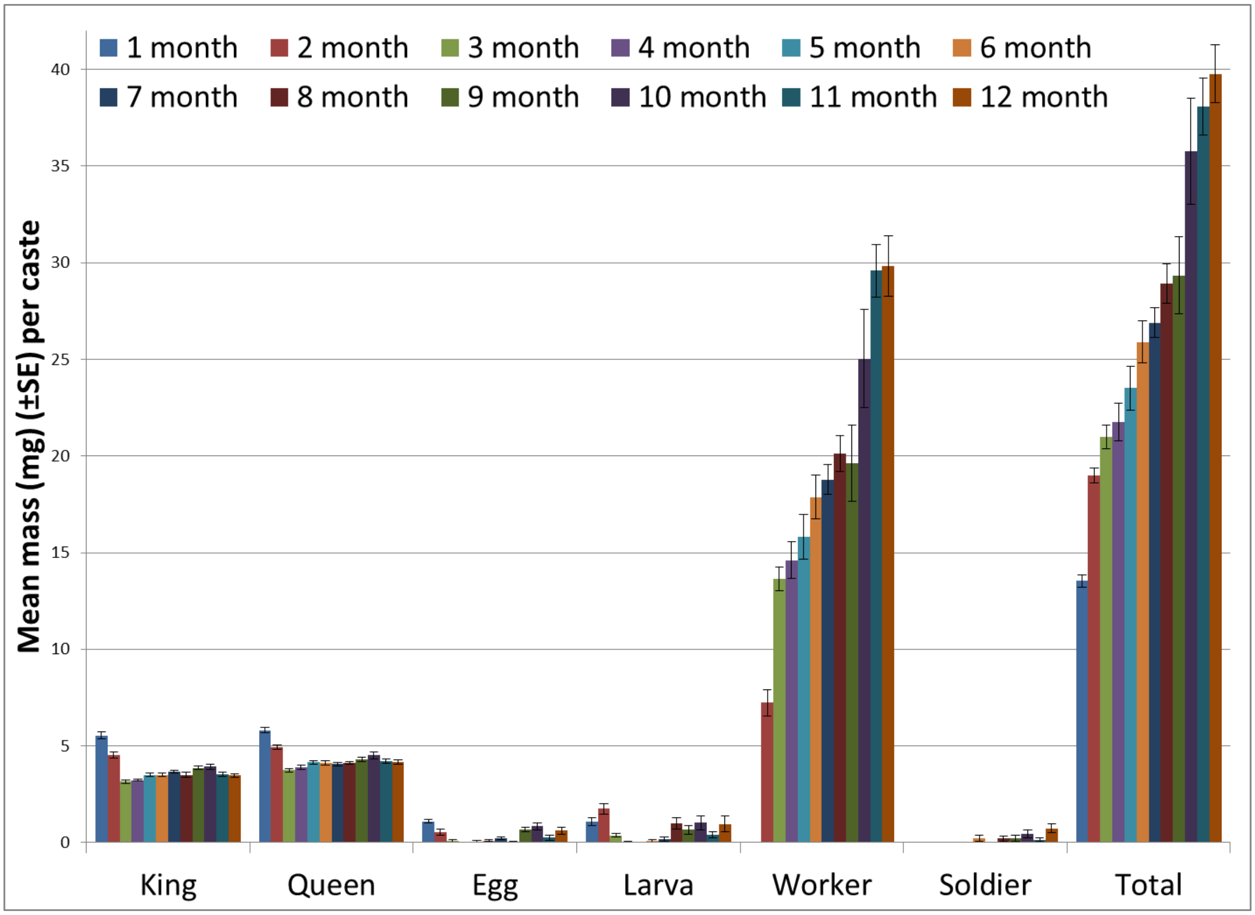

Figure 5. Biomass of Each Caste and/or Developmental Stage at Monthly Intervals During the First Year of Incipient Colony Growth.

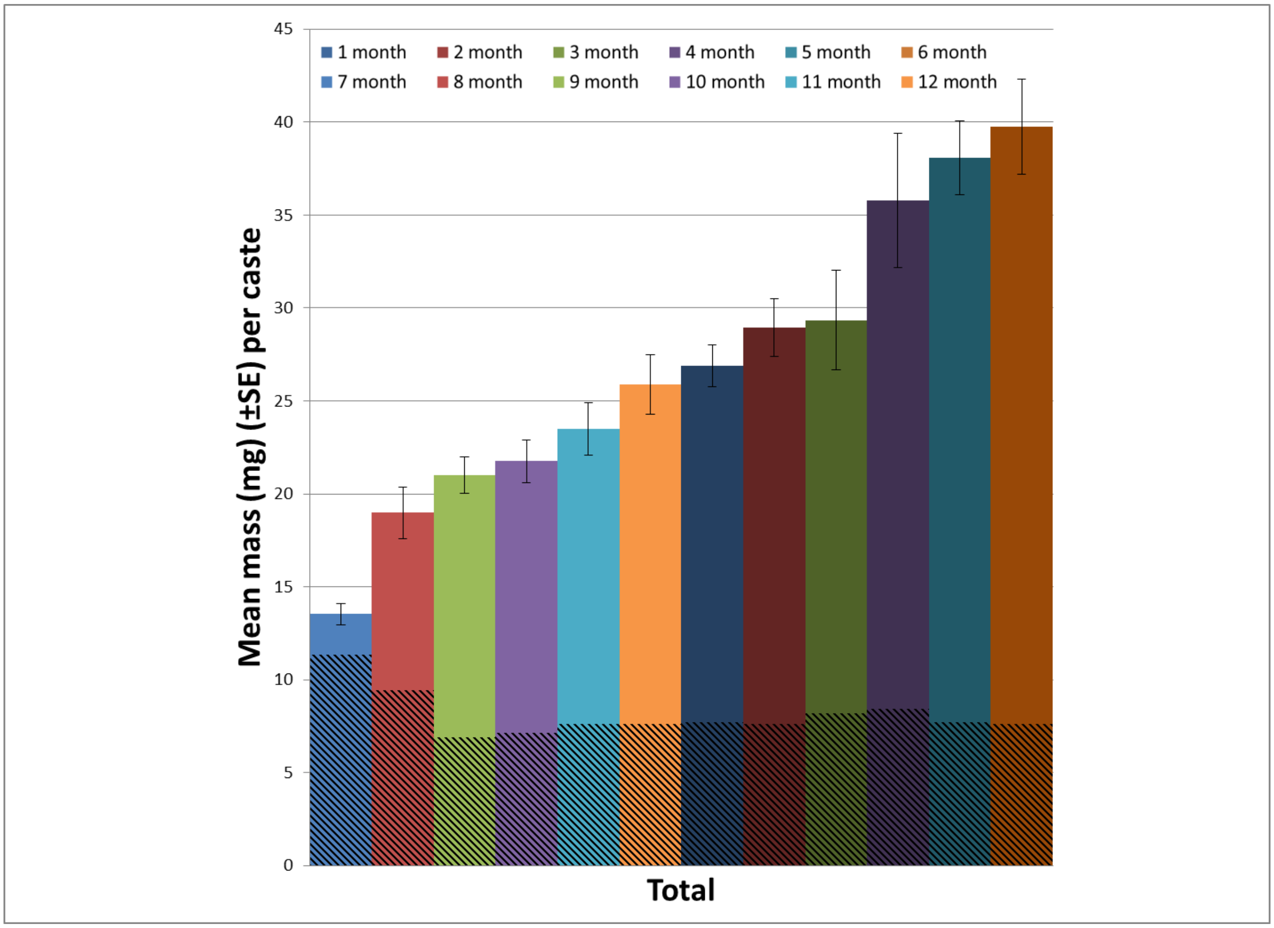

Figure 6. Relative Biomass of Reproductives to Offspring at Monthly Intervals During the First Year of Incipient Colony Growth. The shaded area of each bar represents the reproductives and the non-shaded area represents the offspring.

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